INHERITANCE OF ENDOSPERM TEXTURE IN SWEET × WAXY HYBRIDS OF MAIZE

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Introduction

In a previous publication,[1] the first and second generation of crosses between sweet and waxy varieties of maize were reported and a tentative explanation of their behavior was suggested. It is now possible to add the results of the third season, which to some extent afford a test of the explanation proposed in our first publication.

The immediate result of crosses between the Chinese variety of maize having a waxy endosperm and varieties with sweet endosperm was the production of seeds having a horny endosperm indistinguishable from that of ordinary field varieties of maize. In the second xenia generation all three kinds of endosperm reappeared in the proportion of 9.20 horny, 3.95 sweet, and 2.85 waxy. This ratio was accepted as a 9:4:3 dihybrid ratio. For although the deviations of the individual ears, individual families and the totals were too large to be ascribed to chance, the deviations were not consistently in one direction and to predicate more complicated formulæ would have necessitated different assumptions for different ears. The only interest in treating the problem in this way would be that of solving a mathematical puzzle, for it would be practically impossible to secure individuals enough to test adequately the validity of the assumptions which it would have been necessary to make.

Admitting, then, that the ratios were only an approximation representing a general tendency, it became of

[1] Collins, G. N. and Kempton, J. H., "Inheritance of Waxy Endosperm in Hybrids with Sweet Corn," Circular 120, U. S. Department of Agriculture, Bureau of Plant Industry, 1913.

interest to learn whether predictions were still possible.

For the purpose of making comparisons easy, the original diagram representing the second xenia generation is here repeated. (See Fig. 1.) The meaning of the symbols is as follows: *S* is the factor for sweet, and *X* the factor for waxy. When both *S* and *X* are present the seed is expected to be horny. Small letters indicate the absence or latency of the factors.

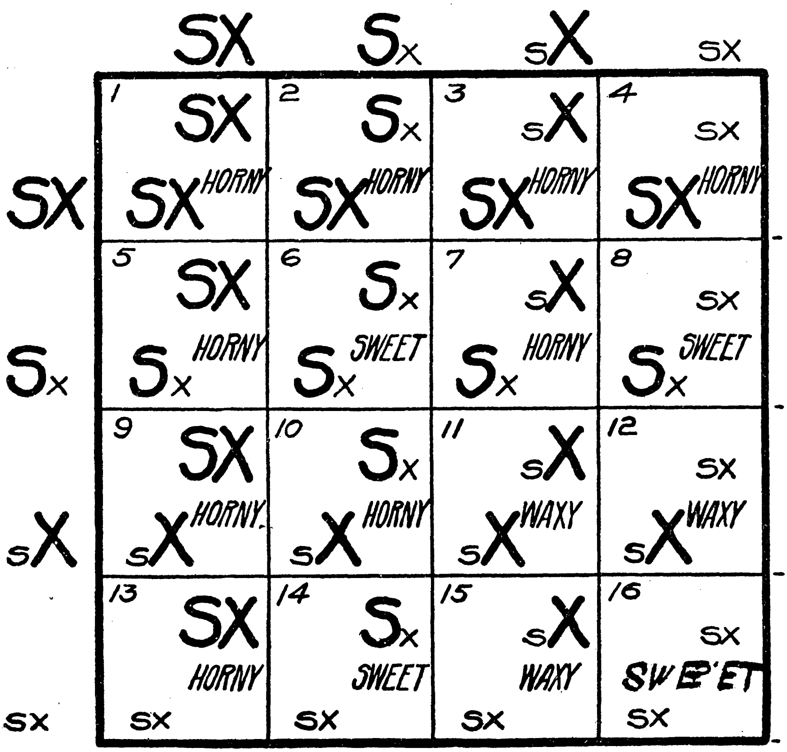

FIG. 1. Diagram showing the gametic composition of second-generation hybrids between waxy and sweet varieties of maize.

Since in both sweet and waxy the alternative factor necessary to produce horny is assumed to be lacking, the gametes produced by sweet varieties are represented by *Sx* and the gametes produced by varieties with waxy endosperm by *sX*. The synthetic horny produced by crossing waxy and sweet is then represented by a combination of

these, or $SxsX$. Assuming a chance recombination of these factors in the gametes derived from these synthetic horny seeds, the gametes will be of four kinds. Both the sweet and the waxy may be present (SX) or the sweet may be present without the waxy (Sx), or the waxy without the sweet (sX), or both may be absent (sx). At fertilization each of these kinds of gametes may unite with any one of the four corresponding kinds derived from the other parent, producing 16 zygotic combinations. In the diagram the four classes of gametes from one parent are given in the horizontal row at the top, and the same four classes from the other parent in the vertical row at the left. Each gametic combination from the top is repeated four times in the squares below, while each combination at the side occurs four times in the corresponding horizontal row of squares. Thus each of the squares represents the result obtained by combining the gametes representing the horizontal and vertical rows that intersect at that point. In all cases where both S and X occur together the seed should be horny, where only S occours the seed should be sweet, when only X occurs it should be waxy, and in one square (No. 16), where neither S nor X occurs there is a new combination which the results have shown to be a new type of sweet seed, indistinguishable from ordinary sweet seed but behaving differently when crossed with other types of endosperm.

In accordance with the above analysis the expected results in the third xenia generation were as follows:

	Proportionate No. of Ears.	Proportions of Seed Classes.
Self-pollinated horny.		
	1	All horny
	2	3 horny: 1 sweet
	2	3 horny: 1 waxy
	4	9 horny: 4 sweet: 3 waxy
Self-pollinated sweet.		
		All sweet
Self-pollinated waxy.		
	1	All waxy
	2	3 waxy: 1 sweet

Crosses between different plants from horny seeds.		
	25	All horny
	20	3 horny: 1 sweet
	20	3 horny: 1 waxy
	16	9 horny: 4 sweet: 3 waxy
Crosses between different plants from sweet seeds.		
		All sweet
Crosses between different plants from waxy seeds.		
	5	All waxy
	4	3 waxy: 1 sweet
Crosses between horny and sweet.		
	3	All horny
	6	1 horny: 1 sweet
	1	1 horny: 1 waxy
	2	3 horny: 1 waxy
	2	1 horny: 2 sweet: 1 waxy
	4	3 horny: 4 sweet: 1 waxy
Crosses between horny and waxy.		
	5	All horny
	4	3 horny: 1 sweet
	10	1 horny: 1 waxy
	8	3 horny: 2 sweet: 3 waxy
Crosses between sweet and waxy.		
	1	All horny
	1	All waxy
	2	1 horny: 1 sweet
	2	1 horny: 1 waxy
	2	1 sweet: 1 waxy
	4	1 horny: 2 sweet: 1 waxy

Third Xenia Generation

Four of the ears bearing second xenia generation seed were selected for planting in 1913, one self- and one cross-pollinated ear from each of the two hybrid families Dh 216 and Dh 221. These families were selected because in 1913 the family Dh 221 showed the greatest deficiency of sweet seeds and Dh 216 was the only family that showed sweet seeds in excess of the expected. The three classes of seeds from each of the ears were planted separately.

Unfortunately as the result of an accident crosses were not made between the plants grown from the different classes, but a total of 77 selfed ears were obtained, a num-

ber sufficient to indicate whether the initial assumption regarding the gametic compositions was of value in arranging the observed facts.

Progeny of Sweet Seeds

Sweet seeds were assumed to result from squares 6, 8, 14 and 16. It will be seen that in none of these is there any factor other than S and since the absence of both factors, as in square 16, is also assumed to produce sweet, we should expect nothing but all sweet ears from self-pollinated plants grown from sweet seeds.

Seventeen self-pollinated ears were secured from plants grown from sweet seeds. All the seeds of these ears were sweet with the exception of one waxy seed. This one waxy seed was colored and since it occurred on an ear from a white sweet seed that otherwise produced only white sweet seeds, the exception may reasonably be ascribed to accidental foreign pollen.

Progeny of Waxy Seeds

Waxy seeds were assumed to have resulted from the combinations shown in squares 11, 12 and 15. Seeds from square 11 should produce only waxy seeds. Squares 12 and 15 should produce ears with waxy and sweet seeds in proportion of 3 waxy to 1 sweet. There should, therefore, be one all waxy ear to two with both waxy and sweet seeds. There were in all 29 ears from waxy seeds, 11 of which were all waxy and 18 with both waxy and sweet seeds. The numbers are small but at least both kinds of ears were secured and the proportion does not violate the original assumption. The 18 ears with both waxy and sweet seeds all produced them in approximately the 3 : 1 ratio. The numbers are given in Table I. The totals with 3,154 seeds indicate that if there is a deviation, it is almost certainly less than 2 per cent.

All the sweet seeds that occur on ears grown from waxy seeds are assumed to belong to the new class of sweet seeds corresponding to that represented in square 16.

Plantings of such seeds are being made for comparison with the ordinary class of sweet seeds having the same ancestry. These are represented by the sweet seeds occurring on ears having horny and sweet seeds.

TABLE I

WAXY SEEDS SELF-POLLINATED. EARS SHOWING WAXY AND SWEET SEEDS. EXPECTED: 25 PER CENT. SWEET

Parent Ear	Pedigree Number	Total No. Seeds	No. Waxy Seeds	No. Sweet Seeds	Per Cent. of Sweet Seeds	Deviation ÷ Prob. Error
Dh 216–1 (Cross-Pollinated)	1938	301	216	85	28.2 ± 1.7	+1.9
	1939	112	85	27	24.1 ± 2.7	− .3
	1940	264	202	62	23.5 ± 1.8	− .8
	1942	18	14	4	22.2 ± 6.6	− .4
	1943	349	258	91	26.1 ± 1.6	+ .7
	1949	149	100	49	32.9 ± 2.6	+3.0
	1950	138	103	35	25.4 ± 2.5	− .2
Dh 216–2 (Self-Pollinated)	1972	389	302	87	22.4 ± 1.4	−1.9
	1973	187	136	51	27.3 ± 2.2	+1.0
	1974	174	138	36	20.7 ± 2.1	−2.0
	1975	85	67	18	21.2 ± 3.0	−1.3
	1976	34	21	13	38.2 ± 5.6	+2.4
	1977	313	232	81	25.9 ± 1.7	+ .5
	1978	109	79	30	27.5 ± 2.9	+ .9
Dh 221–2 (Self-Pollinated)	1994	136	105	31	22.8 ± 2.4	− .9
	1995	155	116	39	25.2 ± 2.3	+ .1
	1996	51	31	20	39.2 ± 4.6	+3.1
	1997	190	146	44	23.2 ± 2.1	− .9
	Total...	3,154	2,351	803	25.5 ± .5	+1.0

PROGENY OF HORNY SEEDS

From the horny seeds the expected results are more complicated. They may be tabulated as follows:

1 ear (Square 1)	with seeds all horny
2 ears (Squares 2 and 5)	with seeds 3 horny: 1 sweet
2 ears (Squares 3 and 9)	with seeds 3 horny: 1 waxy
4 ears (Squares 4, 7, 10 and 13)	with seeds 9 horny: 4 sweet: 3 waxy.

Ears were, therefore, expected in the proportion of 1 all horny ear, 2 with horny and sweet seeds, 2 with horny and waxy seeds and 4 with all three classes. Thirty ears were secured from seed classed as horny. These ears were distributed as follows: 1 all horny, 5 with horny and

sweet seeds, 3 with horny and waxy seeds, 19 with horny, sweet and waxy seeds and *2 all sweet.*

The two all sweet ears are entirely outside the expected. Their appearance may be explained on the assumption that seeds classed as horny in 1912 were in reality sweet. No microscopical examination of the starch was made and the seeds were classified on their appearance, wrinkled seeds being classed as sweet and smooth seeds as horny. The separation of horny from sweet seeds is more difficult to make than waxy from either horny or sweet.[2]

There were, however, very few doubtful seeds in the second xenia generation and in suggesting this interpretation, we may with some propriety be accused of attempting to explain away "green balls."[3]

The two all sweet ears were descendants of an ear Dh 221–2, which showed an excess of horny seeds and a deficiency of sweet. The expected number of sweet seeds in Dh 221–2, which had a total of 493 seeds, was 123 and only 106 were classified as sweet. If this deviation resulted from a faulty classification, that is, if some of the sweet seeds failed to show the characteristic wrinkled exterior, we might expect that about 17 of the 300 seeds classed as horny would produce ears with all sweet seeds. Eleven of the ears secured from horny seeds in 1913 were descendents of this ear.

The remaining 28 ears from horny seeds are distributed among the 3 classes in reasonably close agreement to the expected. Measured by Pearson's formula for the goodness of fit,[4] it appears that such a deviation might be expected once in about twenty times.

[2] The difficulty of distinguishing between sweet and starchy seeds in crosses where the starchy variety has small seeds has been pointed out by East and Hays, "Inheritance in Maize," Bull. 167, Conn. Ag. Exp. Sta., 1911, p. 40.

[3] Pearson, K., and Heron, D., "On Theories of Association," *Biometrika*, IX, pp. 309–314.

[4] *Phil. Mag.*, Vol. L, 1900, pp. 157–175. The application of Pearson's formula to data of this kind was called to our attention by Mr. G. Udney Yule.

The three ears with horny and waxy seeds produced these classes in the expected 3 : 1 ratio. The numbers are given in Table II.

TABLE II

HORNY SEEDS SELF-POLLINATED. EARS SHOWING HORNY AND WAXY SEEDS. EXPECTED: 25 PER CENT. WAXY

Parent Ear	Pedigree Number	Total No. Seeds	No. Horny Seeds	No. Waxy Seeds	Per Cent. of Waxy Seeds	Deviation ÷ Prob. Error
Dh 216–2 (Self-Pollinated)	1962	327	247	80	24.5 ± 1.6	.3
Dh 221–2 (Self-Pollinated)	2000	312	235	77	24.7 ± 1.6	.2
	2007	121	82	39	32.2 ± 2.9	2.5
	Total...	760	564	196	25.8 ± 1.1	.7

Four of the five ears that produced horny and sweet seeds were also as close as could be expected to the 3 : 1 ratio. The fifth, however, Ped. 1965, with 249 seeds, had only 19 sweet seeds or 7.6 per cent. The numbers are given in Table III. The only explanation that can be

TABLE III

HORNY SEEDS SELF-POLLINATED. EARS SHOWING HORNY AND SWEET SEEDS. EXPECTED: 25 PER CENT. SWEET

Parent Ear	Pedigree Number	Total No. Seeds	No. Horny Seeds	No. Sweet Seeds	Per Cent. of Sweet Seeds	Deviation ÷ Prob. Error
Dh 216–1 (Cross-Pollinated)	1965	249	230	19	7.6 ± 1.1	16.0
Dh 216–2 (Self-Pollinated)	1979	442	344	98	22.2 ± 1.3	2.2
Dh 221–1 (Cross-Pollinated)	1988	160	121	39	24.4 ± 2.3	.3
Dh 221–2 (Self-Pollinated)	2003	175	134	41	23.4 ± 2.1	.8
	2008	179	141	38	21.2 ± 2.1	1.8
	Total...	1,205	970	235	19.5 ± .8	6.9

offered in connection with this exceptional ear is that suggested for the occurrence of the two all sweet ears among those grown from seeds classed as horny, namely, the existence of sweet seeds which failed to show a

wrinkled surface. This explanation is rendered less probable, however, by the unusual behavior of the aleurone color in this same ear. In the previous discussion the aleurone color has not been considered. To treat of the aleurone color would naturally lead to the question of correlation between that character and endosperm texture, a subject which in these crosses is very complicated and for the treatment of which the results thus far obtained are inadequate. It may be said, however, that with the exception of Ped. 1965 the proportions of colored to white seeds in all the ears bear out the assumption that the inheritance of the aleurone color is governed by two factors, both of which must be present to produce color. In Ped. 1965, however, which was grown from a colored seed, only 23 of the 249 seeds were white. The colored and white seeds are beautifully distinct with no intermediate or doubtful seeds. The ratio of 9.2 per cent. white might be explained as an approximation to the dihybrid ratio of 6.25 per cent. but we must then admit that instead of both factors being necessary for the development of color either factor alone may produce color.

The 19 ears from horny seeds that showed all three classes are assumed to have the same gametic composition as the original second xenia generation, previously reported. The numbers are given in Table IV. The last column of the table gives the odds in 1,000 that deviations equal to those observed are not chance deviations from the expected proportions, as calculated by Pearson's formula. Thus in Pedigree 1953 the odds are 809 to 191, or practically 4 to 1, that the deviation is not the result of chance.

As in the original ears, the approximation is sufficiently close to render futile any attempt to predicate a different arrangement of factors, but many of the deviations are too large to be ascribed to chance. In the totals the sweet class is too low and the waxy too high, in fact there is no significant difference between the totals for these two classes. The deviation from the expected is, however,

largely the result of two ears Ped. 1954 and 1967, and if the explanation suggested for the two all sweet ears from horny seeds is admitted, it may also account for the deviation in these two ears. In both ears the deficiency of sweet seeds is accompanied by an excess of horny seeds, while in neither ear is there a significant excess of waxy seeds.

TABLE IV

HORNY SEEDS SELF-POLLINATED. EARS SHOWING ALL THREE CLASSES. EXPECTED: 56.25 PER CENT. HORNY, 25 PER CENT. SWEET 18.75 PER CENT. WAXY

Parent Ear	Pedigree	Total No. Seeds	Horny Seeds		Sweet Seeds		Waxy Seeds		Chances in 1000 that the Deviation is not Accidental
			No. Expected	No. Observed	No. Expected	No. Observed	No. Expected	No. Observed	
Dh 216–1 (Cross-Pollinated)	1953	39	22	26	10	5	7	8	809
	1954	350	197	236	87	36	66	78	999+
	1955	198	111	103	50	55	37	40	470
	1956	69	39	42	17	11	13	16	777
	1957	148	83	74	37	42	28	32	664
	1958	176	99	100	44	41	33	35	133
	1963	540	304	289	135	133	101	118	832
	1964	70	39	44	18	8	13	18	983
	1966	170	96	101	42	35	32	34	524
	1967	158	89	108	39	23	30	27	995
Dh 216–2 (Self-Pollinated)	1980	35	20	16	9	11	7	8	486
Dh 221–1 (Cross-Pollinated)	1985	258	145	131	65	73	48	54	784
	1986	120	67	72	30	25	23	23	443
	1987	375	211	201	94	92	70	82	716
Dh 221–2 (Self-Pollinated)	1999	77	43	42	19	16	14	19	676
	2001	27	15	15	7	7	5	5	0
	2002	118	66	71	30	29	22	18	426
	2004	134	75	81	34	29	25	24	455
	2009	79	44	48	20	10	15	21	979
	Total	3,141	1,767	1,800	785	681	589	660	999.99

With these two ears excluded the deviation in the total for the remaining 17 ears may be ascribed to chance. Tested by Pearson's formula such deviations might be expected once in about 50 times.

CONCLUSIONS

The immediate (xenia) result of crossing varieties of maize having sweet and waxy endosperm was the production of seeds with a horny endosperm resembling that of ordinary field varieties. In the second xenia generation all the ears contained seeds of the three classes, sweet, waxy and horny, in fairly definite ratios. The data were arranged in accordance with the Mendelian formula corresponding most nearly to the observed numbers.

The third generation, like the second, gave results sufficiently close to dihybrid ratios to render unprofitable the assumption of more complicated ratios. There are, however, deviations from the expected numbers of too great magnitude to be ascribed to chance.

The ratios of waxy to non-waxy seeds were regular as far as the conditions of the experiment could determine, except for a slight excess in the number of waxy seeds in nearly all the ears in which all three classes appeared (Table IV). A deviation in number of waxy seeds as large as that shown in the total would not be expected to occur as the result of chance more often than once in one thousand times.

The ratios between sweet and horny, while approximating the predicted ratios, show numerous irregularities. Wherever there is a significant deviation in the number of sweet seeds, the observed number is below the expected. Reasons are advanced for believing that the deficiency of the sweet class may result from a failure of some sweet seeds to develop a wrinkled exterior rather than from any irregularities in segregation.

The results show the value of representing the characters by gametic factors. This method provides an orderly arrangement of the facts of heredity thus far observed with respect to these characters and makes possible fairly accurate predictions regarding the genetic behavior of the various seed classes.

WASHINGTON, D. C.,
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